Phylogeny and Evolution of Subterranean and Endogean Cholevidae (= Leiodidae Cholevinae) Proceedings of XX I.C.E. Firenze, 1996 | Mus. reg. Sci. nat. Torino, 1998: 261-286

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Cave and rock debris dwelling species of the *Choleva agilis* species group from central Europe (Coleoptera, Leiodidae: Cholevinae)

ABSTRACT

Five species of the *Choleva agilis* species group have been described in central Europe. They are: the widely distributed and mostly epigean *C. agilis* (Illiger, 1798) and *C. lederiana* Reitter, 1901; alpine rock debris dwelling *C. septentrionis* Jeannel, 1936 from northern Bohemia, Krkonoše Mts.; and two strictly cave dwelling species - *C. holsatica* Benick & Ihssen in Benick, 1937 from northern Germany and *C. gracilenta* Szymczakowski, 1957 from south-eastern Poland. Recently, three other isolated (presently undescribed) populations with relict distributions have been found, in: (1) cold taluses of the České Středohoří Mts., northern Bohemia; (2) caves in Pilis Mts., north-western Hungary; and (3) a cave in Bakony Mts., western Hungary. Multivariate statistical analyses of 19 morphometric characters have been made for samples of all 8 species. These showed (1) gradients of increasing length of appendages (length of antenna, metatibia and metatarsus), and (2) decreasing proportions of eyes and relatively narrow body from epigean to rock debris dwelling to cave dwelling species of *Choleva*. These are interpreted as increasing adaptations to hypogean conditions.

Key words: morphometry, multivariate statistical analysis, hypogean adaptations, Coleoptera, Cholevinae, *Choleva*, central Europe

INTRODUCTION

Small carrion beetles of the subfamily Cholevinae are mostly general scavengers, feeding on carcasses, decaying plant material, fungi and dung (Peck, 1990; Lawrence & Britton, 1994). Many of these species have the tendency to penetrate hypogean habitats and some species are obligate residents of these habitats.

Traditionally, the terrestrial subterranean environment is divided into two groups (Camacho, 1992): (1) caves, including natural cavities, crevices,

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artificial mines etc. (Vandel, 1965); and (2) the superficial underground compartment (also called the MSS, Juberthie et al., 1980a, 1980b, 1981a). Conditions similar to the latter habitat can be also found in some rock debris, taluses and rock fields in mountains as well as in lowlands in cold places (Christian, 1987; Molenda, 1989; Růžička, 1993). However, for animals with small body sizes (like beetles) both habitats sometimes form interconnected systems (Delay & Juberthie, 1981; Racovitza, 1983; Růžička, 1993) which merge into each other.

Two systematic groups of Cholevinae are especially well-known to be related to these habitats: (1) The tribe Leptodirini Lacordaire, 1854 (= Bathysciini Horn, 1880, recently reviewed by Guéorguiev, 1976; Casale et al., 1991). This group contains many mostly Palaearctic species with many morphological as well as physiological and behavioural adaptations (Deleurance-Glacon, 1959; 1963; 1964; Juberthie et al., 1981b; Juberthie-Juppeau, 1988; Juberthie-Juppeau & Cazals, 1984; 1991; 1993). (2) The tribe Ptomaphagini Jeannel, 1911. This has a world-wide distribution, with many species adapted for cave-dwelling in North, Central, and South America (Peck, 1973; 1977; 1984; Gnaspini, 1991; 1993), and one cave-dwelling species in Spain (Blas & Vives, 1983) and several in the Oriental region (Peck, 1981; Perreau, 1993; Zoia, 1994).

A third group, in the tribe Cholevini Kirby, 1837, contains some species, mainly from the genera *Catops* Paykull, 1798 and *Choleva* Latreille, 1796 which obligately dwell in subterranean habitats (Jeannel, 1936; Schweiger, 1950). Many species of *Choleva* are reported from caves (Jeannel, 1923; 1936; Deleurance, 1959; Guéorguiev & Beron, 1962; Beron, 1972; Hubart, 1973; Blas, 1977; 1980; Hippa et al., 1985; Koch, 1989; Růžička & Vávra, 1993), and the superficial underground compartment (Kroker, 1983) and rock debris (Růžička et al. 1989; Molenda, 1989; Růžička & Vávra, 1993; Růžička & Zacharda, 1994), but most of these species are also known to occur in epigean habitats.

One of the exceptions to this pattern of dwelling in both epigean and subterranean habitats is found in some members of the *Choleva agilis* species group. About 11 species are known (Jeannel, 1936; Benick, 1937; Szymczakowski, 1957; Giachino, 1990). From the central European region, two strictly cave-dwelling taxa have been described: *Choleva holsatica* Benick & Ihssen in Benick, 1937 from northern Germany and *Choleva gracilenta* Szymczakowski, 1957 from south-eastern Poland. The known distribution of both species is restricted only to a single cave or to two closely situated and connected caves, respectively. Both species have developed and functional flight wings, but have more elongated appendages, narrower bodies and slightly more reduced eyes compared with their epigean relatives (Benick, 1937; 1939; 1950; Szymczakowski, 1957). Their taxonomic position is not yet stabilized; sometimes both taxa are regarded as subspecies of one or two other Scandinavian species of this group (for detailed discussion about this topic, see Schilthuizen, 1990) and Ipsen this volume.

In recent years, other populations of this group, with very limited areas of distribution, have been discovered in central Europe. One taxon occurs in northern Bohemia, in a few cold taluses of the České Středohoří Mts.; the other two occur in caves in Hungary, in the Pilis and Bakony Mts. (for more detailed locality records, see the data given under sample characteristics below). The *Choleva agilis* species group is now under systematic revision (Růžička & Vávra, in prep.). In this study, all taxa from central Europe are treated as separate species; since all three above mentioned taxa are presently undescribed, in the following text they are referred as to *Choleva* sp. 1 to 3.

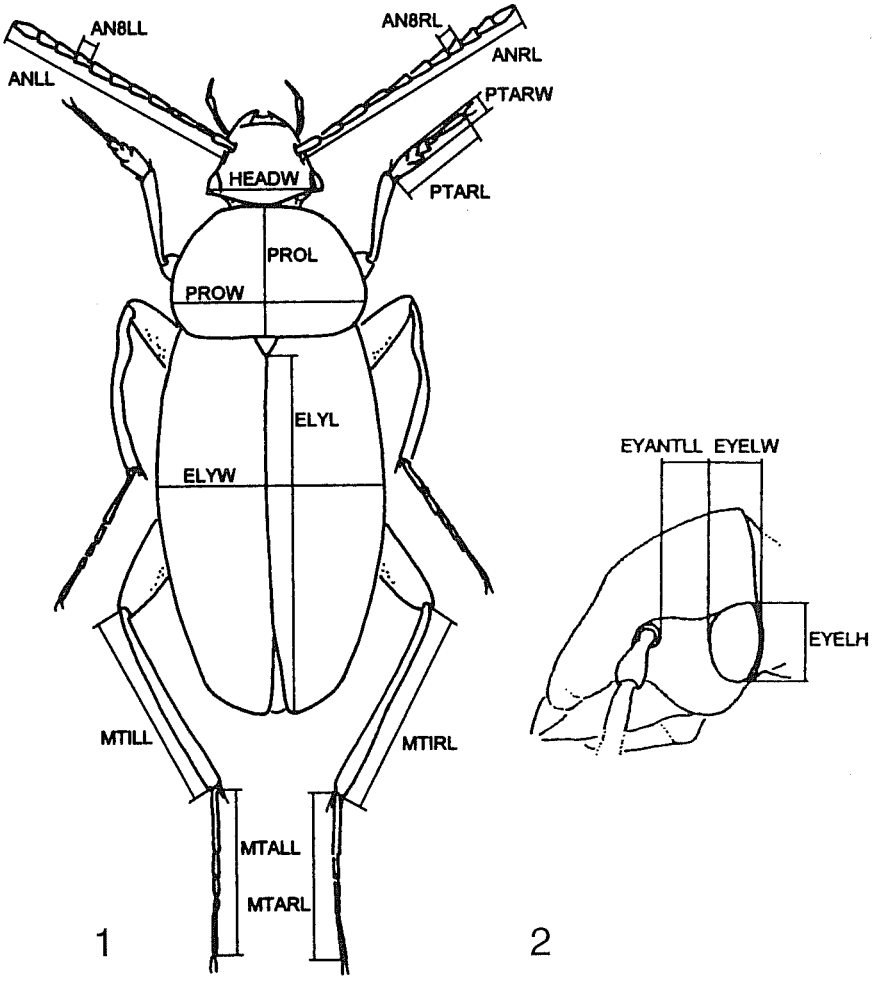
The aim of this paper is (1) to evaluate the importance of selected morphometrical characters for differentiation of central European species of the *Choleva agilis* species group; and (2) to study if some character changes are correlated with the habitat type occupied by species of this group.

Material and methods

The following 21 morphological characters were chosen as variables for morphometrical analyses. They are abbreviated and measured as follows (see also Figs 1-2):

1. PROL - medial length of the pronotum;
2. PROW - maximum width of the pronotum;
3. ELYL - medial length of the elytra from the posterior margin of the scutellum to the elytral tip;
4. ELYW - maximum width of the elytra;
5. ANLL - total length of the left antenna;
6. ANRL - total length of the right antenna;
7. AN8LL - length of the left antennomere 8;
8. AN8RL - length of the right antennomere 8;
9. MTILL - length of the left metatibia;
10. MTIRL - length of the right metatibia;
11. MTALL - length of the left metatarsus (without claw length);
12. MTARL - length of the right metatarsus (without claw length);
13. EYELH - height of the left eye from the lateral view;
14. EYERH - height of the right eye from the lateral view;
15. EYELW - width of the left eye from the lateral view;
16. EYERW - width of the right eye from the lateral view;
17. EYANTLL - the shortest distance between the base of left antenna and anterior margin of the left eye;
18. EYANTRL - the shortest distance between the base of right antenna and anterior margin of the right eye;
19. HEADW - maximum width of the head;
20. PTARL - length of the right protarsus (without claw length);
21. PTARW - width of the basal segment of right protarsus.

For the measurements, an ocular micrometer in a binocular dissecting microscope was used. All characters were measured in an orthogonal view by the same observer; on dry specimens glued on small pinned cards.



Figs 1-2 - Schematic drawings of a *Choleva* specimen, showing the characters selected as morphometric variables: 1 - habitus dorsally, 2 - head laterally. For abbrevations, see Material and methods.

Characters 20 and 21 were measured in male specimens only and were not used in the multivariate methods.

For the morphometrical studies, population samples of the 8 species were chosen from the following localities (the abbreviations for species used through the text and graphs are given first; the number of males and females indicate the number of specimens measured):

1. AGI - *Choleva agilis* (Illiger, 1798) (25 males, 31 females): Bohemia, České Středohoří Mts., Raná hill, 300 m a.s.l., stone accumulation near field, different dates during 1992, pitfall traps, P. Moravec lgt.

2. BAK - *Choleva* sp. 1 (32 males, 27 females): Hungary, Bakony Mts., Pénzesgyör env., Tilos-erdei barlang [cave], 5.iv.-2.viii.1991, pitfall traps, R. Mlejnek lgt.

3. CST - *Choleva* sp. 2 (33 males, 41 females): Bohemia, České Středohoří Mts., Boreč hill, talus on NE slope, 22.iv.-28.v.1993, baited pitfall traps, J. Růžička lgt.

4. GRA - *Choleva gracilenta* Szymczakowski, 1957 (28 males, 26 females): Poland, distr. Częstochowa, Sokole Góry Mts., Pod Sokolą Górą cave, 20.iii.-13.v.1993, pitfall traps, J. Růžička, T. Sitek & J. Vávra lgt.

5. HOL - *Choleva holsatica* Benick & Ihssen in Benick, 1937 (20 males, 30 females): Germany, Schleswig-Holstein, Bad Segeberg, Segeberger Höhle [cave], various dates and collectors (incl. specimens from the type series).

6. LED - *Choleva lederiana* Reitter, 1901 (26 males, 26 females): Finland, Regio aboensis, Lohja, Torhola cave, 22.viii.-30.x.1985, pitfall traps, O. Biström & H. Hippa lgt.

7. PIL - *Choleva* sp. 3 (21 males, 41 females): Hungary, Pilis Mts., Klastrompuszta near Kesztölc, Legény + Leány barlang [caves], 12.v.-5.vii.1989, baited pitfall traps, R. Mlejnek lgt.

8. SEP - *Choleva septentrionis* Jeannel, 1923 (20 males, 26 females): Bohemia, Krkonoše Mts., alpine region, several localities from Vrbatova bouda chalet to Śmielec Mt., 18.vi.-27.viii.1994, baited pitfall traps, J. Janák lgt.

In this study, individual specimens have been considered as operational taxonomic units (OTU's, after Sneath & Sokal, 1973: 69). In total, 453 specimens were measured and used for univariate analyses. However, for multivariate methods only those specimens with no missing body parts were used; this totalled 331.

Individual specimens were grouped using two approaches for analyses. In the first approach, each population sample was classified as a species, and specimens are thus arranged into eight groups. By the second approach, the specimens were a *priori* split into three groups, with reference to the habitats they occupied. These are: (1) Epigean species, usually widely distributed, and often found in tunnels and nests of small mammals. Here belong the spe-

cimens of *Choleva agilis* and *C. lederiana*, although the sample of the latter species was collected in a cave habitat (Biström & Hippa, 1987). However, this species is widely distributed from Scandinavia to central Asia and often found in non-cave habitats (Biström & Väisänen, 1988; Schilthuizen, 1990; Růžička, unpubl.). (2) Species restricted to cold rock debris. Here belong the specimens of *Choleva* sp. 2 (the species known only from a few cold taluses from Bohemia, České Středohoří Mts.); and a central European sample of *C. septentrionis* (known only from taluses and stone fields of alpine habitats in Bohemia, Krkonoše Mts.). (3) Strictly cave-dwelling species. Here belong the specimens of *C. gracilenta, C. holsatica*, and *C.* sp. 1 and *C.* sp. 3 from Hungarian caves.

The statistical analyses were performed using five approaches:

(1) The principal component analysis (PCA) was performed on all 331 beetle specimens and the full set of variables (1 to 19). PCA is an indirect ordination method, which rotates the original coordinate system of N dimensions (N is here the number of variables, i.e. 19) to new orthogonal axes, called principal axes, with the new axes coinciding with directions of maximum variation of the original observations. A low dimensional representation of the data is then provided, because most of the variation between the individuals is contained in the first few linear combinations (Reyment et al., 1984; ter Braak & Prentice, 1988). The $y = \ln (x + 1)$ transformation was applied to the measured data, followed by the centering and standardisation by variables (ter Braak, 1993). Thus the correlation structure of the data was analysed, with the order of magnitudes of individual variables made uniform (Reyment et al., 1984). The specimen - morphometrical variable biplot on the first three PCA axes with specimens grouped to species or to ecological groups was displayed, and 95% envelopes for each group were also marked (Šmilauer, 1993).

(2) The Forward-selection procedure, determining the subset of variables for CVA, was separately performed on the variables, with specimens arranged by species or by ecological groups. This procedure determines the minimal subset of morphometrical variables that best explain the variability between species or ecological groups (ter Braak, 1993). At each step, the variable that adds most to the explained variance of the specimens (expressed here as an additional matrix with binary coded variables for each species or ecological group) is selected. At each step, the Monte Carlo permutation test was used to calculate if the variance of the selected morphometrical variable to be added is statistically significant (ter Braak, 1993). This test does not control the overall size of the test (the total number of variables selected), so the maximum number of morphometric variables was set arbitrarilly to ten. The total p-value required for the full subset of variables was

0.05; thus the p-value for each step is required to be less than 0.005 (for ten variables, 0.05/10 = 0.005). In any case, the Monte Carlo permutation test was performed at each step with 999 permutations. In the analyses, the variable for sex of the individual specimens was coded (1 for males, 0 for females) and included as a covariable in order to eliminate the difference in morphometrical variables 1 to 19 due to sexual dimorphism.

(3) Canonical variate analysis (CVA) was then applied for each subsample of morphometrical variables selected by the above procedure (variables listed in Tables 1,2). This method examines the interrelationships between a number of groups as does the PCA method; but the axes of variation are chosen to maximise the separation between the groups relative to the variation within each of the groups (Reyment et al., 1984). Again, the specimen - morphometrical variable biplot on the first three CVA axes with specimens grouped to species, and specimens - morphometrical variables - ecological group centroids triplot to specimens arranged to ecological groups was then displayed; with 95% envelopes for each group marked (Šmilauer, 1993).

(4) A single factor analysis of variance (ANOVA) for variables and their combinations was then performed. The divisions of specimens to one of the ecological groups were used as the level in ANOVA. Before the analysis, the homoscedasticity of the variable (the homogeneity of variances of each group) was tested using Bartlett's and Hartley's tests (Zar, 1984; Sokal & Rohlf, 1981). When the ANOVA indicated that there was a significant difference between the means of the groups at the 95% level, a multiple comparison analysis was then performed. Because the groups have unequal counts, Scheffé's test was selected (Zar, 1984). Variables with significant differences at the 95% level, arranged in a cline correlated with the ecological groups, are displayed as notched box-and-whisker plots (Koschin et al., 1992).

(5) Finally, hierarchical cluster analysis in Q-mode (study of similarity between pairs of OTU's, here species; Sneath & Sokal, 1973) was performed. This method expresses the overall similarity of the species, using information from the total ordination space (Sneath & Sokal, 1973). The matrix of eight species centroids in the 7 dimensional space limited by a subset of 10 selected morphological variables (listed in Table 1) was used for analysis. An unweighted pair-group cluster analysis with arithmetic averages (UPGMA) was made on the Euclidean distances among each pair of species, and the resulting dendrogram was plotted.

All the calculations for the ordination methods have been performed with the program CANOCO 3.12 (ter Braak, 1993) and the results are displayed using the program CanoDraw 3.0 (Šmilauer, 1993). The univariate analyses were computed and displayed with the aid of STATGRAPHICS 5.0 (using the manual of Koschin et al., 1992). The program NTSYS-pc 1.50 (Rohlf, 1989) was used for the cluster analysis.

RESULTS

Principal component analysis

The first three axes of PCA account for 82.3% of the total variance of the observations (49.9% for the first, 25.8% for the second and 6.7% for the third axis).

For specimens grouped to species, the specimen - morphometrical variable biplot on the first two PCA axes is presented in Fig. 3, and the same on the second and third PCA axis is shown in Fig. 4. Similarly, for the specimens arranged in the three ecological groups, similar results are presented in Fig. 5 and Fig. 6, respectively.

When examining the variables' distribution, we can see that both PROL and ELYL (representing best the total body length) are closely related with the first ordination axis. This axis is often referred as to being considerably influenced by the size factor (Reyment et al., 1984). Also interesting is the close position of variables describing measurements of certain body parts, namely eyes (EYELH, EYERH, EYELW and EYERW), antennae (ANLL, ANRL, AN8LL and AN8RL) and hind legs (MTILL, MTIRL, MTALL and MTARL). Also the width of the body is similar in all three tagmemes (HEADW, PROW, ELYW).

The species groups (Figs 3,4) are rather confused, with a more isolated position only for GRA in the first ordination plane and BAK in the plane defined by the second and third ordination axis.

The relations between variables and ecological groups (Figs 5,6) are also remarkable: the correlations are indicated between the prolongation of appendages (ANLL, ANRL, AN8LL, AN8RL, MTILL, MTIRL, MTALL and MTARL) and the position of cave-dwelling specimen group; and, conversely, correlations are indicated between the enlargement of eyes (EYELH, EYERH, EYELW and EYERW) and the epigean specimen group.

Table 1 - Ten characters taken by the forward-selection procedure for CVA on species. For each step, 999 permutations of Monte Carlo test were performed. See text for more detailed explanation.

var. No.	variable name	F-ratio	p-value
8	AN8RL	40.88	0.001
18	EYANTRL	43.38	0.001
14	EYERH	36.65	0.001
3	ELYL	19.92	0.001
10	MTIRL	23.68	0.001
4	ELYW	23.64	0.001
19	HEADW	16.99	0.001
12	MTARL	16.47	0.001
2	PROW	8.17	0.001
6	ANRL	7.82	0.001

Forward-selection procedure

The ten morphometrical variables best explaining the interspecific variability of specimens are selected and listed in Table 1.

A subset of only 8 morphometrical variables is the best explanation of the variability between the three ecological groups (Table 2). Any of the remaining variables does not significantly increase the explained variance according to the Monte Carlo test.

In both results of this procedure, variables reported as describing similar parts of the body (and closely related according to PCA, see above) were reduced to a single or at least a pair of variables from the subset selected.

Table 2 - Eight characters taken by the forward-selection procedure for CVA on ecological groups. For each step, 999 permutations of Monte Carlo test were performed. See text for more detailed explanation.

var. No.	variable name	F-ratio	p-value
12	MTARL	109.73	0.001
2	PROW	65.94	0.001
18	EYANTRL	31.98	0.001
14	EYERH	35.26	0.001
8	AN8RL	37.02	0.001
19	HEADW	34.59	0.001
16	EYERW	10.24	0.002
4	ELYW	8.14	0.002

Canonical variate analysis

For specimens grouped to species, the specimen - morphometrical variable biplot on the first two CVA axes is presented in Fig. 7, and the same on the first and third CVA axis is shown in Fig. 8. As was expected, the individual species' clouds are more concentrated and better separated from each other than in PCA. The species GRA and BAK are remarkably isolated in the first plane and in the plane spanned by the first and third axis of the ordination space, respectively. The species BAK, GRA, HOL and PIL (all representing cave-dwelling species) are situated on the right side of the ordination planes presented. The species AGI, LED and SEP (all epigean and/or talus-dwelling species) are situated on the opposite, left side of both ordination planes presented; the species CST (characterised by a talus habitat) form a transition between these groups. Again, both groups seem to be related mainly to the elongation of appendages (here represented by the variables AN8RL, ANRL, MTIRL and MTARL); increasing in the first group and

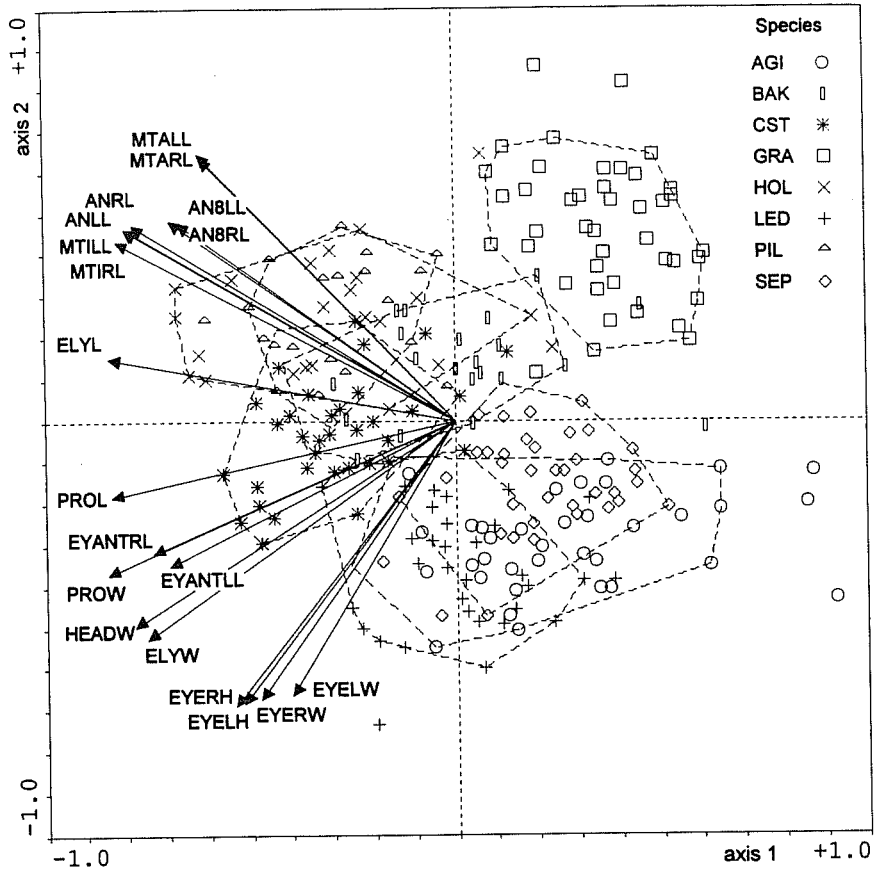


Fig. 3 - Specimen - morphometrical variable biplot on the first two PCA axes. Specimens are grouped to the species, with 95% envelopes marked. For abbreviations, see Material and methods.

decreasing in the later group. The species CST can be characterised by a relatively wide body; whereas the species GRA, by a very narrow body shape (variables HEADW, PROW and ELYW).

For specimens arranged according to ecological groups, the specimens - morphometrical variables - ecological groups triplot on the first two CVA axes is presented in Fig. 9. In these graphs are added also the positions of group centroids. The specimens of the cave-dwelling species are nearly com-

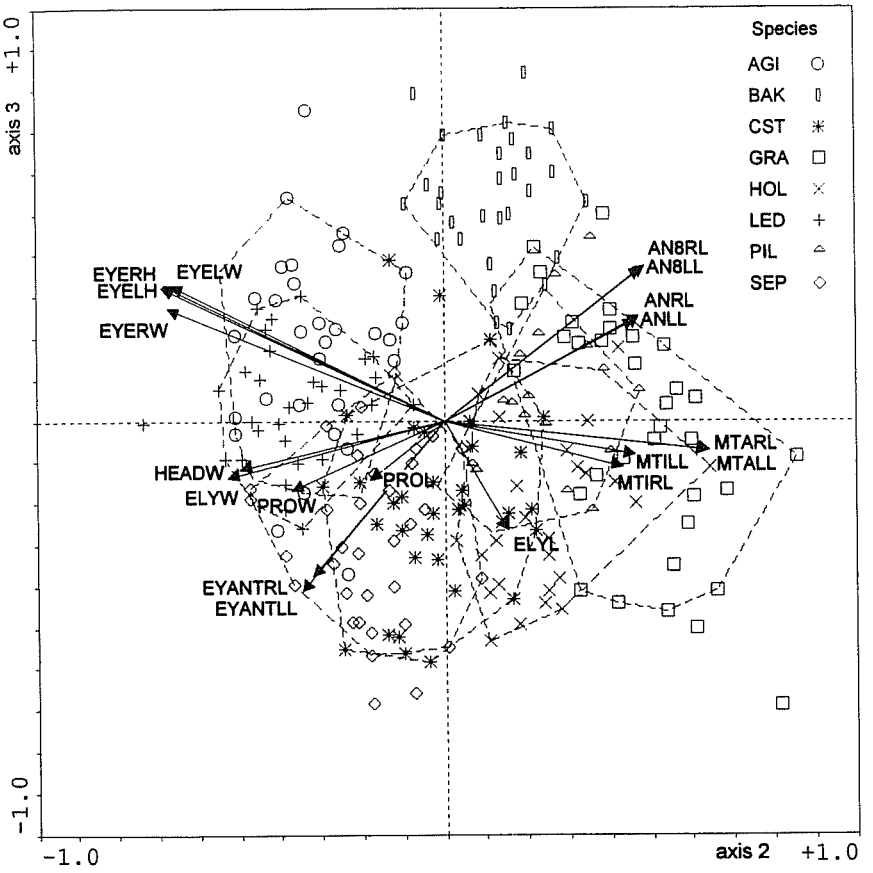


Fig. 4 - Specimen - morphometrical variable biplot on the second and third PCA axis. Specimens are grouped to the species, with 95% envelopes marked. For abbreviations, see Material and methods.

pletely isolated on the left side of the first ordination plane. The groups of specimens from the epigeon and taluses are much more overlapped, yet situated mainly on the right side. In this ordination, again, cave-dwelling specimens seem to be correlated with the prolonged appendages (here variables AN8RL and MTARL); talus-dwelling species with increasing width of the body (e.g., variables HEADW and PROW); and epigean specimens with larger eye size (variables EYERH, EYERW).

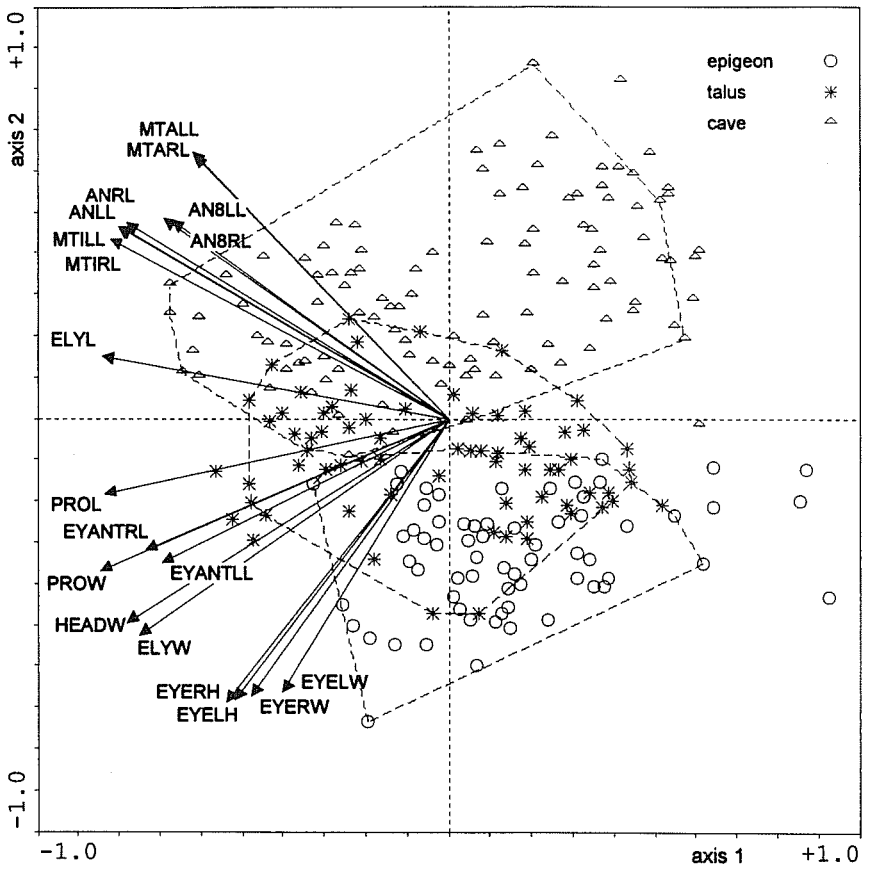


Fig. 5 - Specimen - morphometrical variable biplot on the first two PCA axes. Specimens are arranged to the ecological groups, with 95% envelopes marked. For abbreviations, see Material and methods.

variable name	B. t.	ANOVA	sign. level	multiple range analysis (Scheffé's test) epigeon-talus	epigeon-cave	talus-cave
ANRL	*	75.911	***	*	*	*
AN8RL	*	114.094	***	*	*	*
MTIRL	*	64.092	***	*	*	n.s.
MTARL	*	191.391	***	*	*	*
EYERH	*	39.299	***	*	*	*
EYERW	*	56.032	***	*	*	*
ANRL+MTIRL+MTARL / PROL+ELYL	*	170.937	***	*	*	*
EYERW / PROL+ELYL	*	95.135	***	*	*	*
PROL+ELYL / ELYW	*	127.206	***	*	*	*
PTARL / PTARW	*	26.399	***	n.s.	*	*

Table 3 - Univariate ANOVA of selected morphometrical variables and their ratios between the three ecological groups (e.g., d.f. = 2 for all rows). B.t. means Bartlett's test; *** - significance at $p < 0.0001$, * - significance at $p < 0.05$. For abbreviations for variables, see Material and methods.

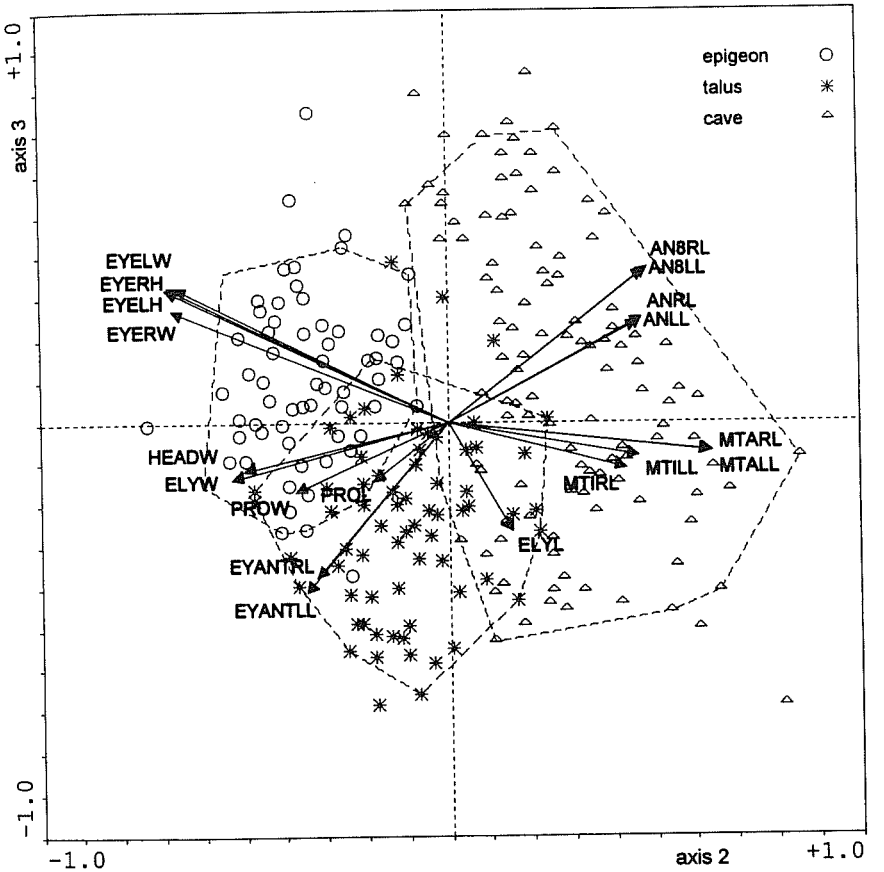


Fig. 6 - Specimen - morphometrical variable biplot on the second and third PCA axis. Specimens are arranged to the ecological groups, with 95% envelopes marked. For abbreviations, see Material and methods.

A single factor analysis of variance

From the variables studied (No. 1 - 19), the six which most significantly display the absolute differences in variable lengths for separate ecological groups are figured in Figs 10-15 (the display of related tests can be observed in Table 3). In absolute measurements (given uniformly in mm), the value of the length of appendages (here ANRL, AN8RL and MTARL) are significantly increasing in specimens from epigeon to talus to cave habitat (Figs 10,11,13). For MTIRL, the epigean specimens have significantly lower values than beetles from talus or cave; however, the difference in lengths of MTIRL between these groups is not significant at the 95% level (Fig. 12;

Table 3). Conversely, the absolute proportions of eyes (represented by EYERH and EYERW) are significantly increasing along this ecological gradient (Figs 14,15).

Also, the relative values of these variables significantly differ in individual groups arranged along the same gradient. The joint lengths of appendages (expressed here as sum of ANRL, MTIRL and MTARL) and the width of eyes (the variable EYERW), both divided by the body length (represented here as sum of PROL and ELYL) display similar results to those of absolute lengths (Figs 16,17). Also the ratio of body length (again, represented by the sum of PROL and ELYW) to body width (ELYW) indicate a significant narrowing of body shape along this ecological gradient. However, neither the

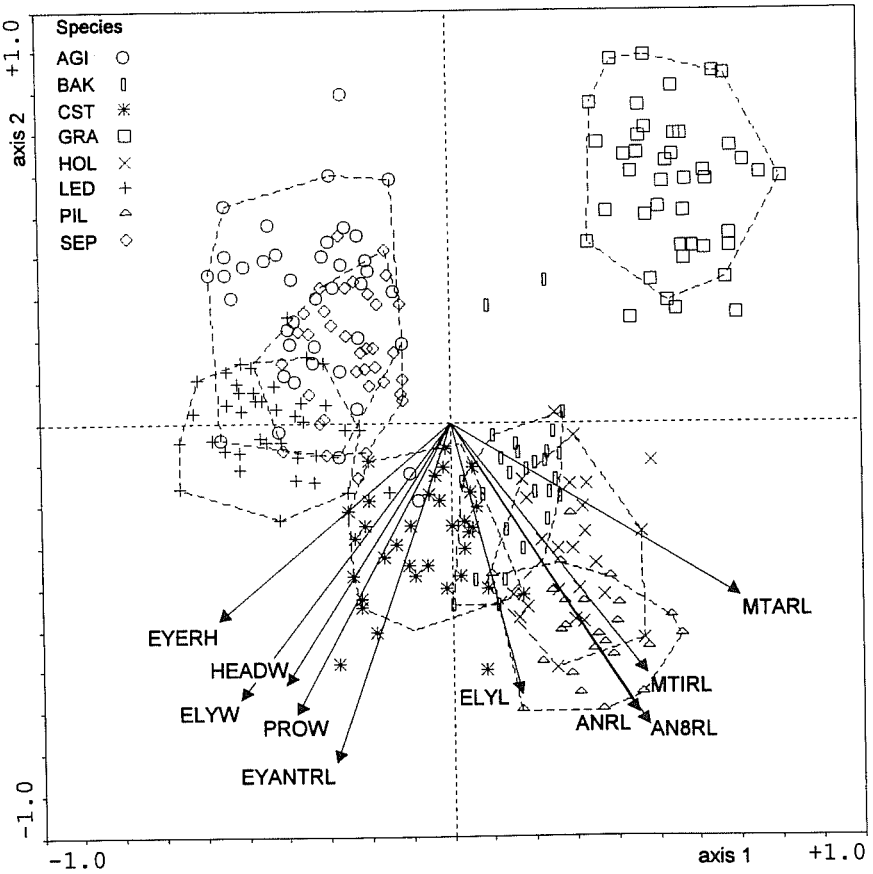


Fig. 7 - Specimen - morphometrical variable biplot on the first two CVA axes. Only 10 most significant variables are selected using forward-selection procedure for specimens grouped to species, 95% envelopes for species are marked. For abbreviations, see Material and methods.

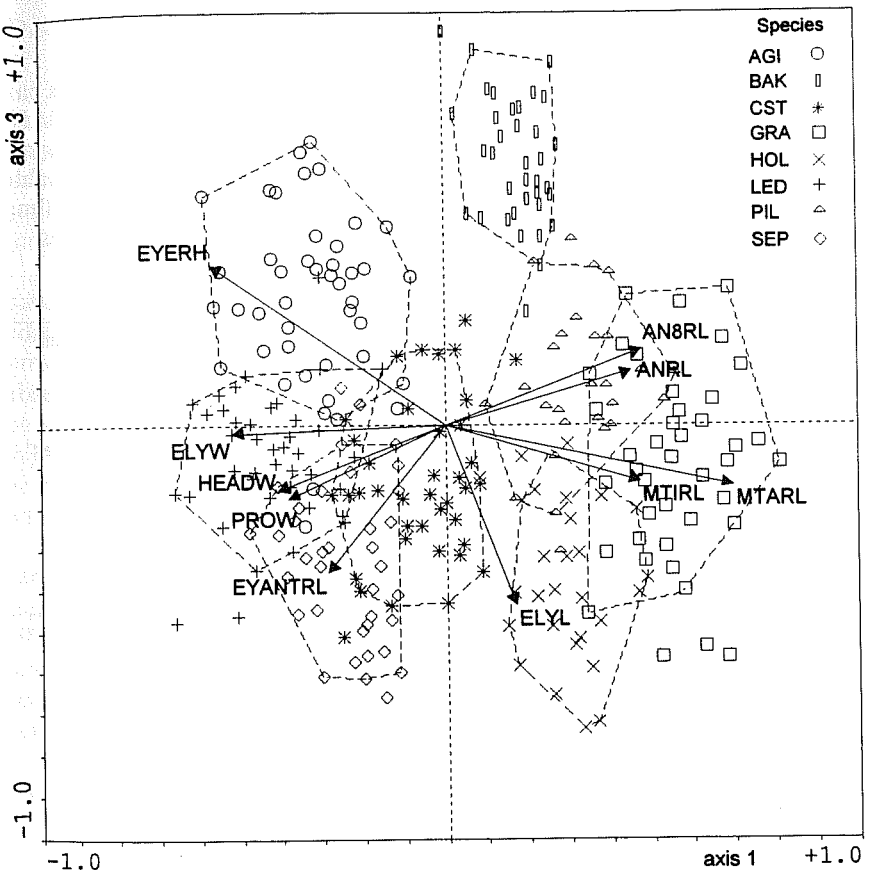


Fig. 8 - Specimen - morphometrical variable biplot on the first and third CVA axis. Only 10 most significant variables are selected using forward-selection procedure for specimens grouped to species, 95% envelopes for species are marked. For abbreviations, see Material and methods.

differences in body length alone (expressed as sum of PROL and ELYW) nor the body width alone (variable ELYW) is significantly (at $p = 0.05$) arranged along such a gradient. Finally, the ratio of protarsus length to width (the quotient of PTARL by PTARW) shows a significant prolongation of the protarsus in specimens from caves when compared with those from taluses or the epigeon (Fig. 19). However, at the level $p = 0.05$, there is not a significant difference between specimens from both these different habitats (see also Table 3).

Cluster analysis

The resulting dendrogram is plotted in Fig. 20. Four distinct groups can be observed: most isolated is the position of species GRA, followed by BAK. The third group is composed of two species, viz. HOL and PIL. The last group is formed by the cluster CST + (AGI + (LED + SEP)). Also notable from this is that the species from the first three groups are all cave-dwelling and the last group being a mixture of talus-dwelling and epigean species.

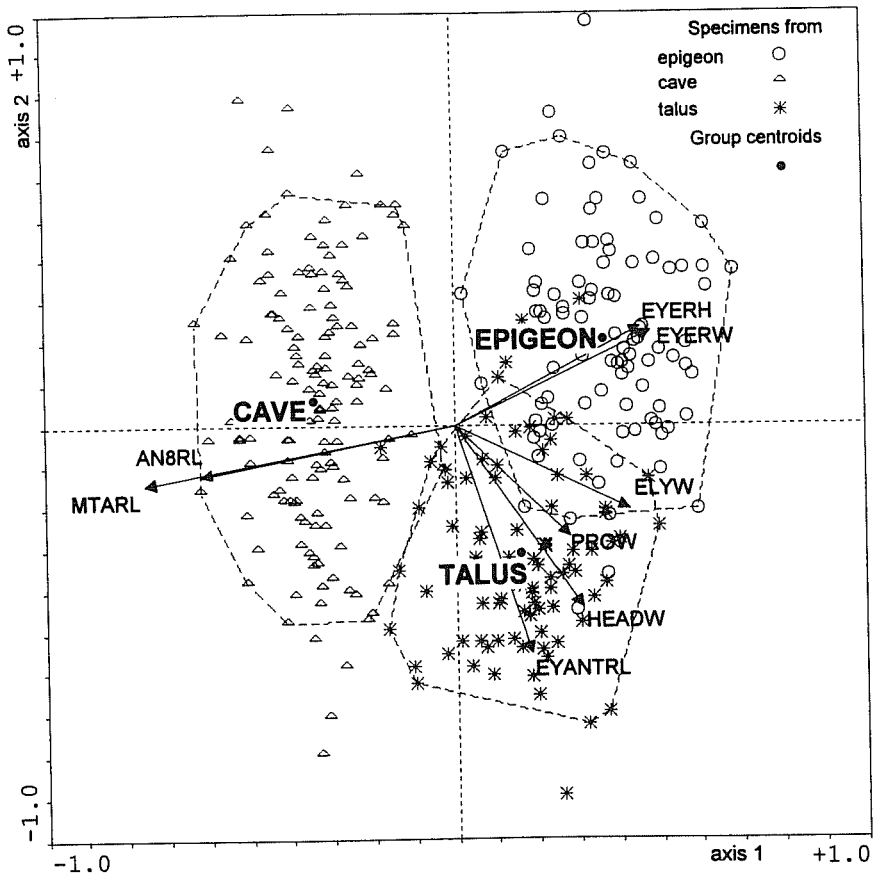


Fig. 9 - Specimen - morphometrical variable - ecological group triplot on the first two CVA axes. Only 8 most significant variables are selected using forward-selection procedure for specimens arranged to ecological groups, 95% envelopes for ecological groups are marked. For abbreviations, see Material and methods.

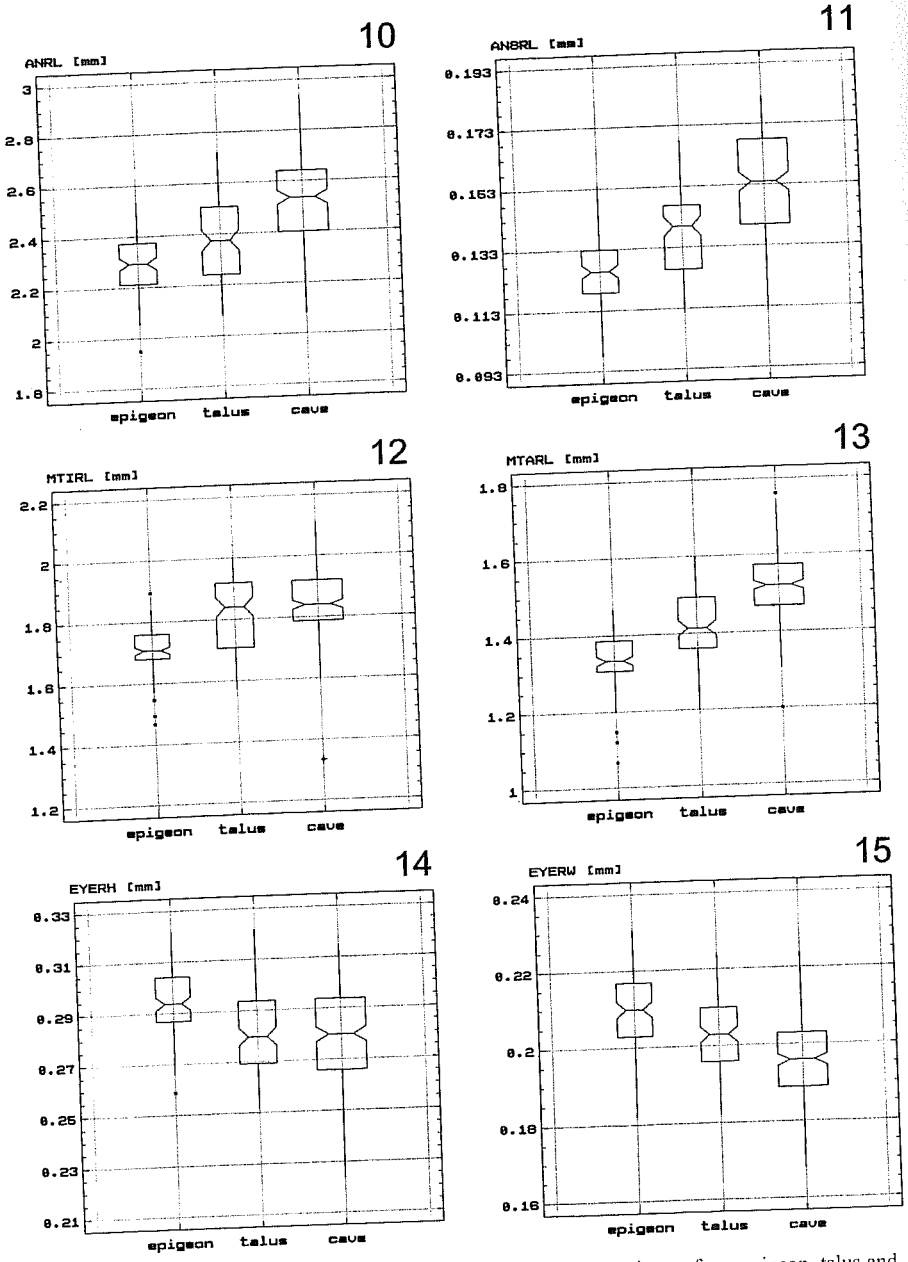
Discussion

Morphological modifications are found in the many and various organisms living in caves (usually called troglomorphies: Christiansen, 1992); the major features found in adults of cave-dwelling arthropods have been summarised in Christiansen (1992) as: the elongation of appendages; specialisation of sensory organs; foot modifications; reduction of eyes, wings, pigment; cuticle thinning; pseudophysogastry.

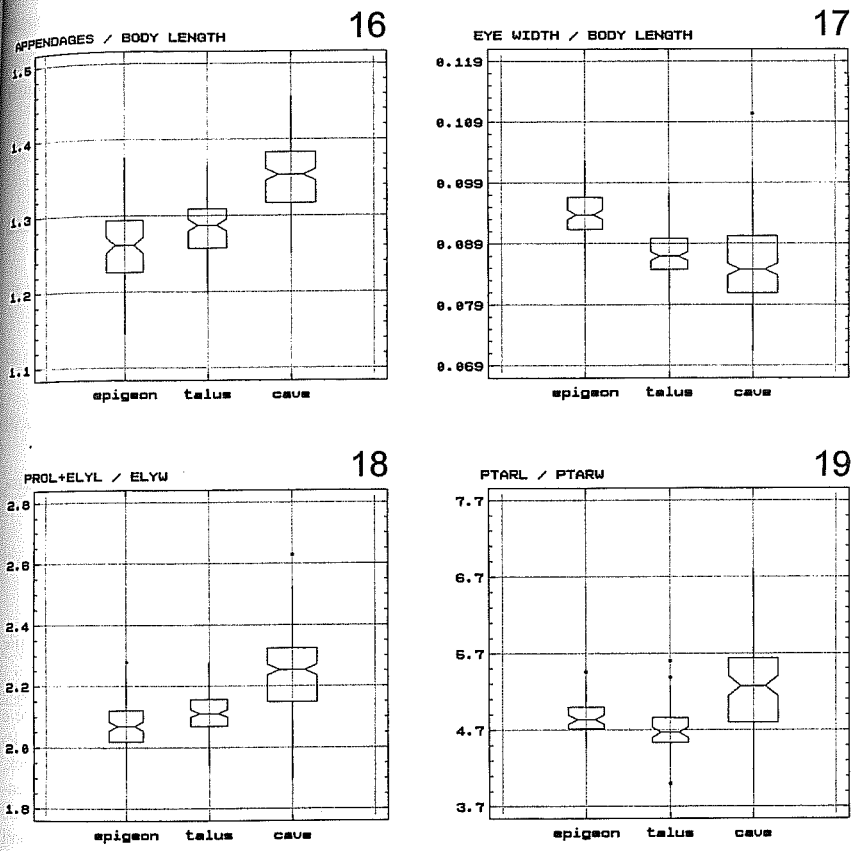
Two main models of modifications for regular cave inhabiting species have been proposed: (1) The morphological differences are the result of adaptations, which evolved by natural selection. The important selective pressures in the evolution of cavernicoles have been considered to be the absence of light, the reduced and irregular food supply and the constant temperature and humidity of subterranean habitats, in particular (Poulson & White, 1969). (2) Random processes like genetic drift and genetic bottlenecks may also play an important role in producing the pattern of differentiation among populations (Caccone, 1985; Ridley, 1993).

Morphometric analyses of cave-dwelling species of Cholevinae have mostly been performed on Leptodirini (Coiffait et al., 1963; Juberthie et al., 1980c; Gers, 1983; Crouau-Roy 1989; Tizado et al., 1997) and Ptomaphagini (Peck, 1986). In these, the cave-dwelling species or populations are found to be differentiated from those from superficial underground compartment or epigeon; the modifications seem to agree with some of the above mentioned general morphological features. Furthermore, past studies using univariate data also indicate moderate changes in some characters of cave-dwelling species of the *Choleva agilis* species group (Benick, 1937; 1939; 1950; Heun, 1955; Szymczakowski, 1957). They are confirmed here by results obtained from multivariate procedures. Thus, because similar patterns of modification are observed in different phylogenetic groups in Cholevinae and also in different geographical regions, it is probable that these features are at least partially the result of adaptational processes.

The study of morphometrical characters in different populations of epigean, talus and cave inhabiting species of *Choleva* is only the first approach to mapping the paths of evolution in this group. If some homoplasies (similar modifications of the same character) in this case are in fact influenced by convergent selection pressures, then they may be supported or refuted by the study of the pattern of meristic, non-morphometrical (structural and/or genetical), and reproductive characters; and comparing the results of this contribution with further cladistic analysis.



Figs 10-15 - Notched box-and-whisker plots of six variables for specimens from epigeon, talus and cave habitats. For abbreviations, see Material and methods.



Figs 16-19 - Notched box-and-whisker plots of four variable ratios for specimens from epigeon, talus and cave habitats. For abbreviations, see Material and methods.

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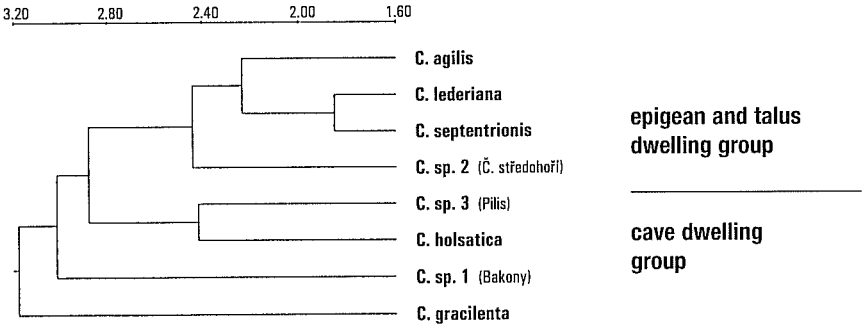

Fig. 20 - Dendrogram from UPGMA cluster analysis of Euclidean distances between centroids representing separate species. For abbreviations used for species samples, see Material and methods.

RIASSUNTO

Specie cavernicole e degli sfasciumi rocciosi del gruppo di Choleva agilis *in Europa Centrale (Coleoptera: Leiodidae: Cholevinae)*

Dell'Europa Centrale sono state descritte cinque specie appartenenti al gruppo di *Choleva agilis*. Rispettivamente: *C. agilis* (Illiger, 1978) e *C. lederiana* Reitter, 1901, largamente distribuite e prevalentemente epigee; *C. septentrionis* Jeannel, 1936, di Krkonoše Mts. in Boemia settentrionale, specie tipica degli sfasciumi rocciosi in ambiente alpino; *C. holsatica* Benick & Ihssen in Benick, 1937 della Germania settentrionale e *C. gracilenta* Szymczakowki, 1957 della Polonia sud-occidentale, ambedue strettamente cavernicole. Recentemente, tre popolazioni isolate con distribuzione relitta (ancora da descrivere) sono state scoperte in: ammassi franosi freddi negli České středohoří Mts. nella Boemia settentrionale; grotte nei Pilis Mts. nell'Ungheria nord-occidentale; in una grotta nei Bakony Mts. nell'Ungheria occidentale. Un'analisi statistica multivariata su 19 caratteri morfometrici è stata condotta su campioni di tutte e 8 le specie. Queste mostrano un gradiente crescente della lunghezza delle appendici (lunghezza di antenne, metatibia e metatarsi), un gradiente decrescente delle dimensioni degli occhi e un corpo relativamente più stretto nel passaggio: specie epigee - specie degli sfasciumi rocciosi - specie cavernicole. Questa situazione viene qui interpretata come un incremento nell'adattamento all'ambiente ipogeo.

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